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Phosphorus restriction influences P efficiency and ornamental quality of poinsettia and chrysanthemum

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ABSTRACT

Better synchronization of plant-available phosphorus (P) with crop P requirement is required to reduce P losses to the environment and to improve resource-efficiency of the exploitation of non-renewable phosphate rock. In horticultural plant production, a restricted availability of P may limit stem length and improve compactness, which are desirable characters for many ornamental plants. In the present study, we investigated the effect of reduced availability of P on plant quality, biomass production and phosphorus efficiency of poinsettia (*Euphorbia pulcherrima* cv. 'Mira Red') and chrysanthemum (*Chrysanthemum* × *morifolium* cv. 'Breeze Cassis'). Five P concentrations (6, 12, 18, 24 or 48 mg L^{-1}) were applied as starter P in the peat-based potting substrate as well as in the nutrient solution given during the experiment. Stem length of both plant species was strongly restricted at 6 mg P L^{-1} but was not significantly affected by higher P levels. For poinsettia, the optimum bract diameter was obtained at 18 mg P L^{-1}. For maximum shoot dry biomass, branching and plant diameter, however, 24 mg L^{-1} was needed. Optimal plant diameter and shoot biomass of chrysanthemum was obtained at 18 mg P L^{-1} while 24 mg L^{-1} was required for maximum flower number. Increasing the P supply to 48 mg L^{-1} did not improve shoot dry matter, branching or flowering of either species, but induced luxury uptake of P. Total shoot P uptake increased linearly over the P fertilizer range tested. For optimal plant biomass combined with optimal ornamental quality, shoot P concentrations at 90 DAP was in the range of 0.30-0.35 % for poinsettia and 0.25-0.30 % for chrysanthemum. Chrysanthemum showed a higher phosphorus efficiency than poinsettia at low P levels, mainly related to a higher internal P utilization efficiency. The P acquisition efficiency was in the range of 55–60 % for both species, and was not significantly affected by the total amount of P applied. In conclusion, with the P fertilization strategy used, P restriction could not be used for plant height restriction of poinsettia "Mira Red" or chrysanthemum "Breeze Cassis" without negative effects on plant quality. However, P fertilization could be markedly reduced without negative effects on plant growth and development, improving phosphorus efficiency and recovery.

1. Introduction

Phosphorus (P) is a non-renewable resource with a limited geographic distribution (Cordell and White, 2014; Van Kauwenbergh, 2010). At the same time, in many areas the widespread use of P fertilizers have increased the P contents in agricultural soils, leading to increased P loss and problems with eutrophication and algal blooms in lakes and estuaries/coastal sea areas (Ulén et al., 2007; Elser et al., 2007; Schindler et al., 2016). Hence, it is important to use P fertilizer restrictively and in accordance with the requirement of the crop (Withers et al., 2014) to economize with a limited resource and reduce the negative environmental effects.

A restricted availability of phosphorus (P) has been reported to produce shorter and/or more compact plants (Baas et al., 1995; Hansen and Nielsen, 2001; Petersen and Hansen, 2003; Hansen and Petersen, 2004; Nowak, 2001; Nowak and Stroka, 2001; Nelson et al., 2012; Liptay and Sikkema, 2000; Frantz, 2013; Justice and Faust, 2015). For example, phosphorus deficiency reduced both plant height and fresh weight for *Pelargonium zonale*, *Petunia*, *Salvia splendens*, *Impatiens walleriana* and poinsettia (Baas et al., 1995). Increasing compactness with a decreasing level of substrate P was observed for a number of bedding plants (*Gomphrena globosa*, *Impatiens walleriana*, *Petunia* × *hybrida*, *Tagetes erecta*) cultivated in peat:perlite and fertigated with 0, 3.4, 6.5 or 21.7 mg P L^{-1} (Nelson et al., 2012).

Developing alternatives to chemical plant growth regulators (PGRs) for controlling shoot length in potted plant production is important to

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reduce the risks of negative effects on human health and on the environment (Hjollund et al., 2004). The availability of PGRs is restricted in several countries, due to the aforementioned risks. Besides manipulation of climatic factors such as temperature, daylength, light spectral composition and relative air humidity (Bergstrand, 2017), restricting the availability of water and/or plant nutrients (Alem et al., 2015; Hansen and Nielsen, 2001; Petersen and Hansen, 2003; Hansen and Petersen, 2004; Nowak, 2001; Nowak and Stroka, 2001) have been suggested as alternative methods for the production of more compact potted plants. A limited supply of P often favour root growth over shoot growth (Hansen et al., 1998; Kim and Li, 2016) and may increase root length per unit plant biomass and improve root distribution (Hansen and Lynch, 1998). Limited P fertilization may also improve drought stress tolerance (Borch et al., 2003) and increase post-harvest quality (Hansen and Nielsen, 2001; Petersen and Hansen, 2003; Hansen and Petersen, 2004).

A main challenge is to limit plant height and shift the root:shoot ratio towards plant root development without obtaining unwanted effects like reduced shoot branching (Baas et al., 1995), reduced bud formation (Baas et al., 1995; Justice and Faust, 2015) or delayed flowering (Kageyama and Konishi, 1992; Justice and Faust, 2015). This means that the soil solution P concentration needs to be strictly controlled (e.g. Hansen and Nielsen, 2001; Justice and Faust, 2015). Plant P requirement, however, is highly dependent on plant developmental stage (Khandan-Mirkohi and Schenk, 2009b; Frantz, 2013; Kim and Li, 2016). For chrysanthemum and poinsettia, P is mainly retranslocated from the shoot to the reproductive organs in the generative stage (Hansen and Lynch, 1998; Henry et al., 2018). Khandan-Mirkohi and Schenk (2009b) noted that both the relative growth rate and the maximum root P uptake rate (I_{max}) of poinsettia, as well as the required concentration of P in the substrate, decreased with increasing plant age. Also for lantana, the P requirement was higher in the vegetative, linear growth phase than in the reproductive stage (Kim and Li, 2016).

A strict regulation of substrate P concentration is important not only to control plant quality but also to reduce the risk of negative effects on the environment. Losses of P from agriculture is an important contributor to eutrophication and algal blooms in freshwater ecosystems and coastal waters (Ulén et al., 2007; Elser et al., 2007; Schindler et al., 2016). In potted plant production, more P fertilizer is commonly added compared with the amount required by the plants (Hansen et al., 1998; Frantz, 2013; Kim and Li, 2016). Commonly used fertilizers added initially at $1-2\,kg\ m^{-3}$ of substrate will give from 45 to 90 to $70-140\,mg\ P\ L^{-1}$ (Sonneveld and Voogt, 2009). A survey of fertilized potting substrates from commercial Swedish growers showed P concentrations from 60 to $100\,mg\,L^{-1}$ (Bergstrand, unpublished). In addition to the initial substrate fertilization, a nutrient solution P concentration in the $30-60\,mg\,L^{-1}$ range is recommended for many potted plants (Sonneveld and Voogt, 2009). As soilless media have a limited capacity to retain P (Marconi and Nelson, 1984), there is a high risk for leakage (Marconi and Nelson, 1984; Ku and Hershey, 1996, 1997; Ristvey et al., 2007). Several authors have suggested that P fertilization of ornamental plants could be reduced compared with recommendations (e.g. Ku and Hershey, 1996, 1997; Hansen et al., 1998; Frantz, 2013; Kim and Li, 2016). However, a prerequisite for better P management in ornamental production systems is more information on the P requirements of ornamental crops (Kim and Li, 2016).

The concept of *phosphorus efficiency* (PE) can be used to evaluate and compare the ability to efficiently use phosphorus by crop species. PE can be defined as the ability to produce yield or biomass under certain available P supply conditions (Wang et al., 2010). PE is determined both by the amount of P taken up by the plant per unit of phosphorus added (*P acquisition efficiency*, PAE) and by the amount of dry matter produced per unit of P taken up (*internal P utilization efficiency*, PUE). Plants have several mechanisms for increasing PAE when the availability of P is restricted. At low P in the root zone, the proportion of fine roots and the number of root hairs may be increased, high-affinity P transporters may be induced, and the exudation of organic acids, phosphatases and other compounds that can improve P solubility and plant P availability may increase (Ramaekers et al., 2010). While PAE has been more intensively studied, PUE has also been suggested to be a significant bottleneck for improvements in the P efficiency of crop plants (Wang et al., 2010).

Limited information on PE, PA and PUE is available for ornamental crops. Frantz (2013) discussed the influence of P treatments on vinca and zinnia in relation to PE and PAE. PAE has also been reported for azalea (Ristvey et al., 2007) while Kim and Li (2016) investigated the PUE of *Lantana camara*. However, as ornamental quality can be expected to be of greater interest to the consumer and grower than biomass yield *per se*, the application of the PE concept is not as straightforward for ornamental plants as it is for edible crops.

The purpose of our study was to investigate if a restricted supply of P could be used to control stem length of poinsettia and chrysanthemum without negatively affecting flowering or other parameters affecting ornamental quality. We also wanted to evaluate and compare the efficiency of P acquisition and internal P utilization as a complement to the evaluation of quality parameters. Optimizing the use of P for ornamental crop species with regard to plant quality as well as to P efficiency would be beneficial both for the environment and for the grower.

2. Materials and methods

2.1. Experimental design

Two pot experiments, one with poinsettia and one with chrysanthemum, were conducted with five different initial P fertilizer levels (6, 12, 18, 24, $48\,mg\,L^{-1}$) in the growing substrate. The nutrient solution used for fertigation during the cultivation period contained the same P concentration as was initially added to the respective substrate (6, 12, 18, 24, $48\,mg\,L^{-1}$). The P treatments and the total amounts of P applied are summarized in Table 1. Both experiments were conducted as completely randomized designs and included 10 replicate pots per treatment.

2.2. Substrates

The substrate consisted of 100 % light block peat (0 − 10 mm; Dragamyr, Mullmäster) supplemented with $1.0\,kg\ m^{-3}$ of lime, $2.5\,kg\ m^{-3}$ of dolomite, and $60\,kg\ m^{-3}$ of Bara EDR clay (Bara Mineraler AB, Bara, Sweden). Besides the P treatments, the substrate was fertilized with N: 120, K: 247, Mg: 42, S:57, Fe: 2, B: 0.27, Mn: 0.6, Cu: 0.2, Zn: 0.27, Mo: $0.04\,mg\,L^{-1}$. P was applied at 6, 12, 18, 24 or $48\,mg\,L^{-1}$ in the form of KH_2PO_4, and the amounts of K and S were balanced with K_2SO_4 and $CaSO_4$. The mean initial $pH_{(H2O)}$ of the fertilized substrates was 5.0 ± 0.1.

Table 1
The concentrations of P ($mg\,L^{-1}$) in the substrate at the start of the experiment (Substrate) and in the weekly fertigation solution (Fertigation), and the total amount of P (mg) applied per plant during the experiment, in the different P treatments for poinsettia and chrysanthemum.

P treatment	6	12	18	24	48
P concentration, mg L^{-1}					
Substrate	6	12	18	24	48
Fertigation	6	12	18	24	48
Total amount of P applied per plant, mg					
Poinsettia	8.76	17.52	26.28	35.04	70.08
Chrysanthemum	7.56	15.12	22.68	30.24	60.48

2.3. Cultivation

Poinsettia: Rooted cuttings of poinsettia (*Euphorbia pulcherrima* cv. 'Mira Red') were transplanted to 12 cm pots containing 235 g of fertilized substrate at the 1 st of September. The poinsettias were cultivated as non-pinched, single-stem plants.

Chrysanthemum: Rooted cuttings of chrysanthemum (*Chrysanthemum* × *morifolium* Ramat. cv. 'Breeze Cassis') were transplanted to 12 cm pots containing 235 g of fertilized substrate at the 9th of September. On September 12, the plants were pinched over five nodes.

Both experiments were performed in a research greenhouse chamber at Alnarp, Sweden (55 °N, 13 °E). The greenhouse was a wide-span greenhouse with covering material Plexiglas® SDP 16/980 (Röhm, Darmstadt, Germany). The plants were grown at 18 °C heating temperature, with vents opening when temperature exceeded set-points by 2 °C. Both the poinsettia and the chrysanthemum plants were exposed to natural light and daylength until October 12th when they were subjected to short photoperiod (10 h) by covering with black plastic screens.

The plants were watered individually with 100 mL of water as needed. Leaching from the pots were prevented by plastic saucers in the poinsettia, but not in the chrysanthemum experiment. During the first two (chrysanthemum) or four (poinsettia) weeks, each pot received a weekly dose of 100 mL of a 0.1 % $Ca(NO_3)_2$ solution. Fertilization with a complete nutrient solution with the same composition and P treatments as described for *Substrates* above started at 36 and 28 DAP, respectively, for poinsettia and chrysanthemum. For the next five (chrysanthemum) or seven (poinsettia) weeks, each pot received 100 mL of a complete nutrient solution with the same composition as above, but with N increased to 260 mg L^{-1}. The amount of K in the different P treatments was balanced with K_2SO_4. Due to the differences in cultivation period, the total amount of P received by chrysanthemum corresponded to 86 % of the amount that was given to poinsettia.

2.4. Plant measurements and analyses

The experiments were harvested on November 29 (89 DAP, poinsettia) and December 8 (91 DAP, chrysanthemum). For poinsettia, stem length from soil surface to apex, stem diameter, plant diameter, lateral shoot number, node number, bract number and diameter were measured. The plant and bract diameters were measured with a ruler, from leaf tip to leaf tip at the widest location. For chrysanthemum, plant diameter and the number of shoots per plant were registered. Stem length and node, bud and flower numbers were measured on each of the three longest shoots above the pinching position. Internode length was calculated by dividing stem length with the number of nodes.

Total shoot fresh weights, as well as dry matter content (DM) after drying at 70 °C for at least 72 h, were determined. Within each treatment, the dried shoots from nine replicates were pooled to three samples, each consisting of the shoots from three plants. A subsample from each pooled sample was digested in HNO_3 in a microwave accelerated reaction system (CEM Mars5) and the P concentration was measured by Inductively Coupled Plasma Emission Spectroscopy (ICP-ES) by Eurofins Agro Testing Sweden, Kristianstad.

2.5. Phosphorus efficiency

Phosphorus efficiency (PE) was estimated as the amount of shoot dry matter produced per unit of P supplied. Internal P utilization efficiency (PUE) was calculated as the amount of shoot dry matter per mg of P taken up in the shoot. Phosphorus acquisition efficiency (PAE) was estimated as the total shoot P content divided with the total amount of P supplied. The initial P content and DM of the transplants were estimated from the regression equations and subtracted before calculation of PE, PAE and PUE.

2.6. Statistics

Residuals were plotted to check the assumptions for the analysis of variance and the results were analysed by one-way ANOVA (SAS Institute, Inc.) for each plant species. Treatment means were separated by Tukey's HSD test ($p < 0.05$). Relations between P variables were evaluated with Pearson's correlation coefficient. Linear regression was performed for the parameters shoot DM, shoot total P uptake and shoot P concentration against the total amount of P applied. For shoot DM, segmented regression was used to identify the breakpoint; i.e. the amount of P fertilizer where no further dry matter increase could be observed. As the mean values observed for shoot dry matter at 24 and 48 mg P L^{-1} were not significantly different, the slope was set to zero for the second segment of the curve. For the P concentration, segmented regression was used to identify the shoot concentration corresponding to the breakpoint estimated from the shoot dry matter response.

3. Results

3.1. Plant ornamental quality and biomass

3.1.1. Poinsettia

The vegetative characters stem length, stem diameter, plant diameter, lateral shoot number, node number and internode length were all affected by the P treatment ($p < 0.001$). Stem length (Fig. 1A), internode length (Fig. 1B), node number and stem diameter (data not shown) increased when P was raised from 6 to 12 mg L^{-1}, while no significant effect was obtained by higher P levels. In contrast, plant diameter (Fig. 1C) and lateral shoot number (Fig. 1 D) increased significantly with increasing P up to 24 mg L^{-1}.

The generative characters bract number and bract diameter were also affected by the P level ($p < 0.05$). Bract number (data not shown) and bract diameter (Fig. 1E) were significantly larger at 12 and 18 mg P L^{-1}, respectively, compared with 6 mg L^{-1}, but tended to decrease from 24 to 48 mg L^{-1}.

Poinsettia shoot DM was also strongly affected by the P treatment ($p < 0.001$) and increased significantly with an increasing level of P added up to 24 mg L^{-1} (Fig. 2A). The breakpoint identified by segmented regression for the response of shoot DM against the amount of P fertilizer applied was 37 mg P. For the first linear segment, the slope was 0.14 g DM mg^{-1} of P added.

In contrast to shoot DM, shoot FW continued to increase with P up to 48 mg L^{-1} (data not shown). The percentage of the maximum FW (at 48 mg L^{-1}) that was produced at the lower P levels was 36, 56, 69 and 93 % at 6, 12, 18 and 24 mg L^{-1}, respectively. Shoot dry matter content was significantly lower at 48 mg L^{-1} (15.9 %) than at 6 (18.0 %) or 12 (17.3 %) mg L^{-1}.

3.1.2. Chrysanthemum

For chrysanthemum, stem length, internode length, plant diameter ($p < 0.001$) and the number of shoots ($p < 0.01$) were all affected by the P treatment. Similar to poinsettia, chrysanthemum stem length was significantly lower at 6 mg L^{-1} compared with the other P treatments (Fig. 1F). Internodes, however, were shorter at 48 mg L^{-1} than at 6, 12 and 18 mg L^{-1} (Fig. 1G). Maximum plant diameter was obtained at 18 mg L^{-1} (Fig. 1H), while the number of shoots was higher at 24 and 48 compared with 6 mg L^{-1} (Fig. 1I).

Chrysanthemum flower + bud number was significantly higher at 24 and 48 than at 6 mg L^{-1} (Fig. 1J). Bud colour was visible 4–7 days later for 6 mg L^{-1} compared with the other P treatments.

Chrysanthemum shoot DM was also strongly affected by the P treatment ($p < 0.001$; Fig. 2D). The breakpoint determined by segmented regression for the response of shoot DM against the amount of P fertilizer applied was 18 mg P L^{-1}. For the first linear segment of the curve, the slope was 0.31 g DM mg^{-1} of P.

Similar to poinsettia, shoot fresh weight (FW) increased up to

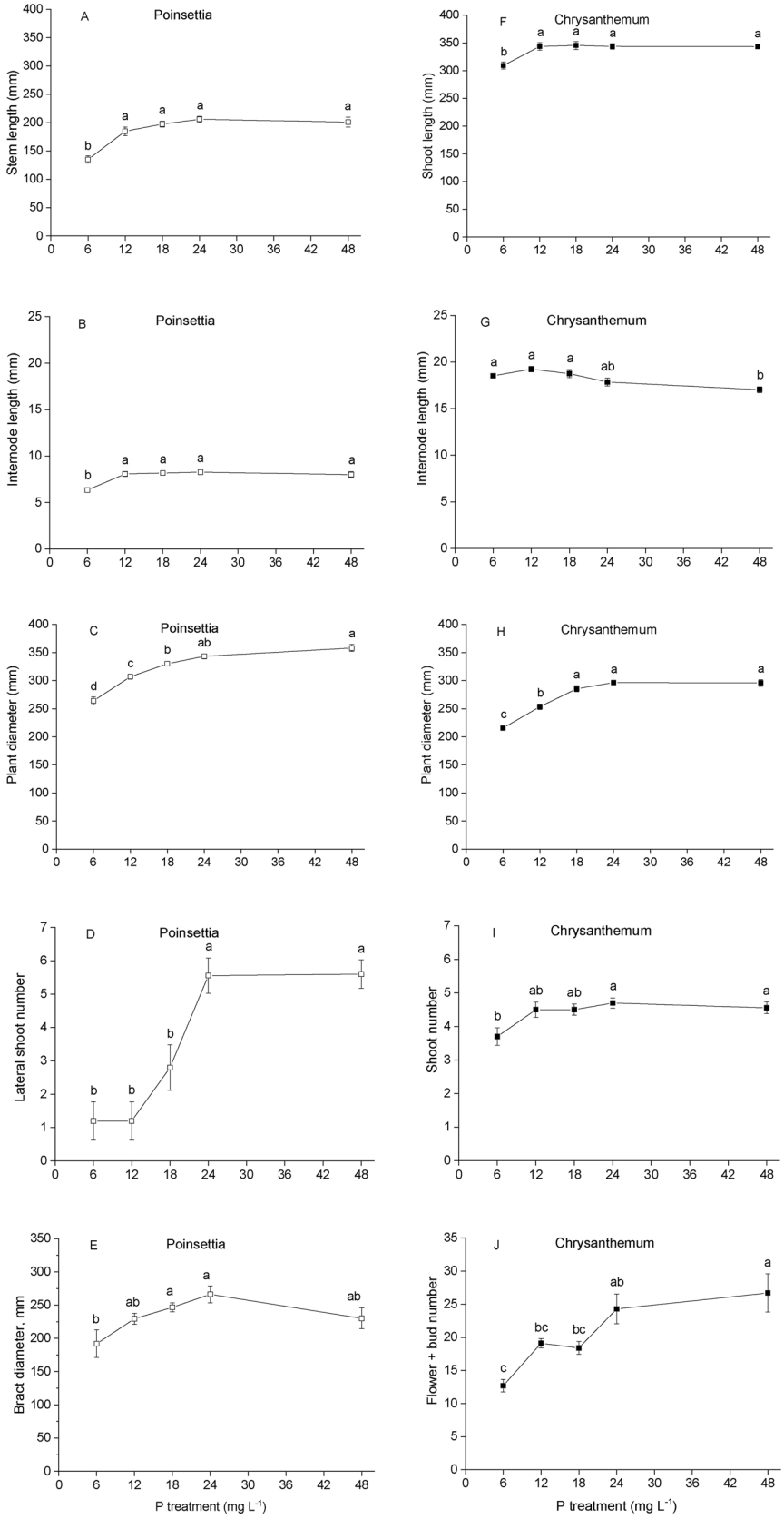

Fig. 1. Mean stem and internode length, plant diameter, shoot number and bract diameter/flower + bud number as functions of the phosphorus treatment (mg P L^{-1} of substrate at start as well as mg P L^{-1} of fertigation solution) for poinsettia and chrysanthemum.

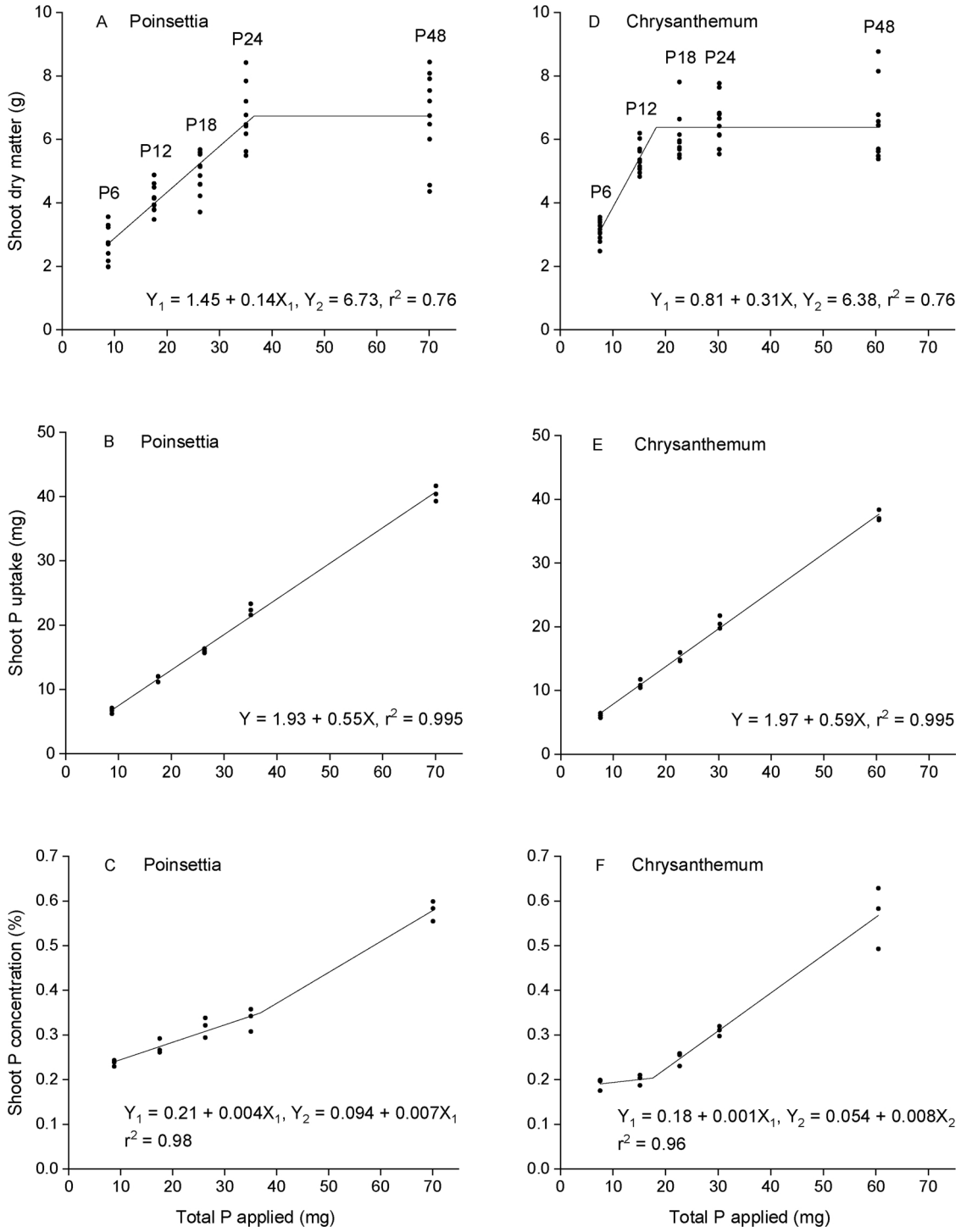

Fig. 2. Total shoot dry matter (n = 10), total shoot P uptake and shoot P concentration (n = 3) as functions of the total amount of fertilizer P applied during the experimental period for poinsettia and chrysanthemum. The response curves were estimated by segmented (A, C, D, F) and linear (B, E) regression, respectively. The corresponding P treatments are shown above the respective data points in the graphs of the upper row.

48 mg P L^{-1} (data not shown). The percentage of the maximum FW (at 48 mg P L^{-1}) that was obtained at the lower P levels was 49, 84, 91 and 96 % at 6, 12, 18 and 24 mg L^{-1}, respectively. For chrysanthemum, the percentage of shoot dry matter (11.1 %) was not significantly affected by the P treatment.

3.2. Shoot P concentration, accumulation and efficiency

3.2.1. Poinsettia

For poinsettia, the P treatment markedly affected total shoot P uptake (Fig. 2B) and shoot P concentration (Fig. 2C), PE (Fig. 3A) and PUE (Fig. 3C) ($p < 0.001$). The total shoot P uptake increased linearly with P ($R^2 \geq 0.995$, $p < 0.001$). For shoot P concentration, a slow rise in the 6–24 mg P L^{-1} range was followed by a stronger increase when P was doubled from 24 to 48 mg L^{-1}. When the 37 mg of P estimated as

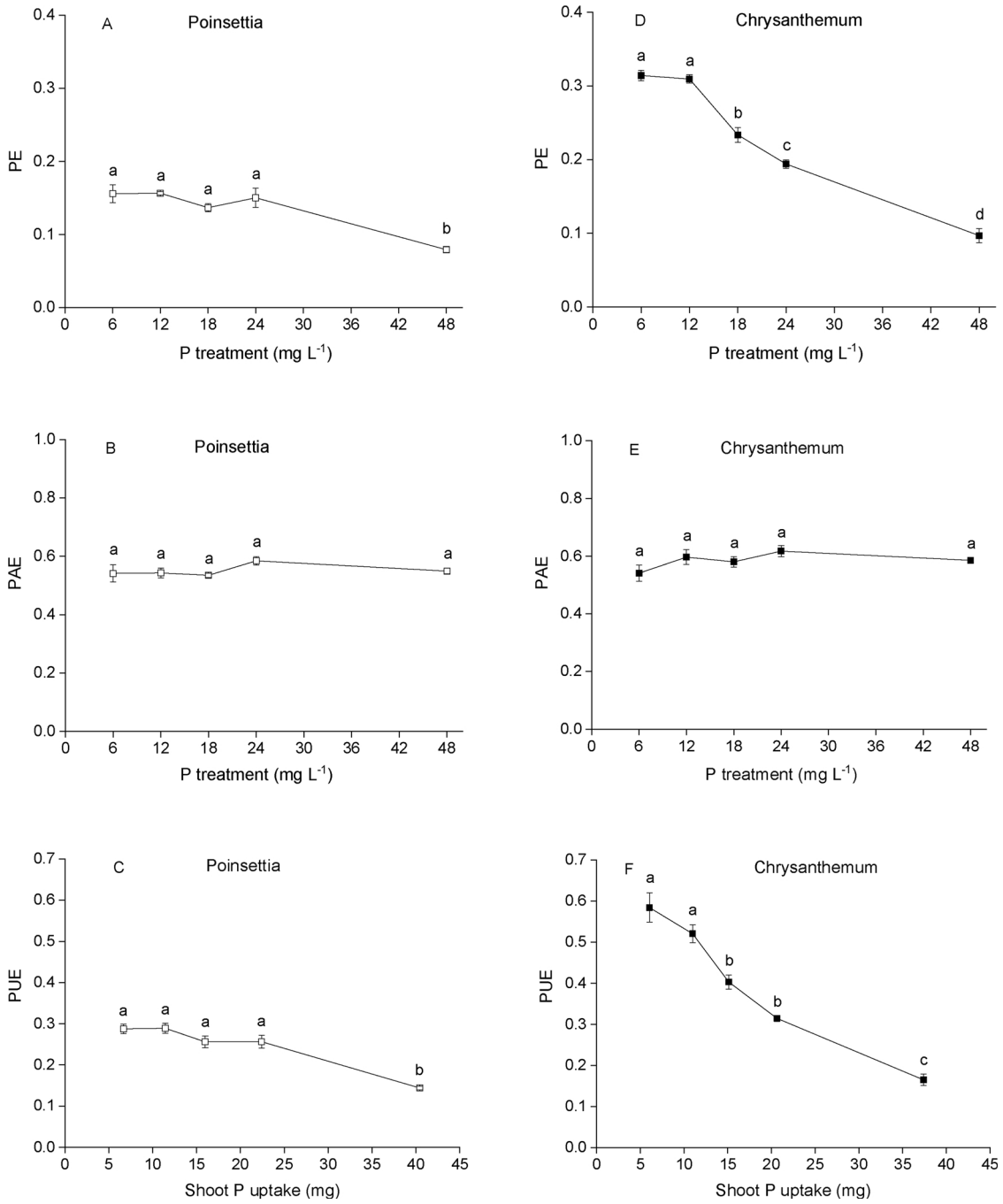

Fig. 3. Shoot phosphorus efficiency (PE) and phosphorus acquisition efficiency (PAE) as functions of P treatment, and shoot phosphorus utilization efficiency (PUE) as a function of total shoot P uptake, for poinsettia and chrysanthemum (n = 3).

necessary for optimal shoot dry matter (see 3.1) was used as a fixed breakpoint in segmented regression, the corresponding P concentration was estimated to 0.35 %. The intercept of the first segment with the Y-axis was 0.21 %. Shoot DM was positively correlated with both shoot P uptake ($r = 0.89$, $p < 0.001$) and shoot P concentration ($r = 0.79$, $p < 0.001$). The intercept with the Y-axis for shoot P uptake indicated that 1.93 mg P was already present in the plantlets at the start of the experiment. This amount was subtracted from the total P uptake when PE and PAE were calculated.

Shoot P efficiency (PE) generally decreased with an increasing amount of P applied; from 0.16 g DM mg^{-1} P at 6 and 12 to 0.08 g DM mg^{-1} P at 48 mg P L^{-1} (Fig. 3A). The P absorption efficiency (PAE) was in the range of 0.54-0.58 mg shoot P per mg of P fertilizer added and did not differ significantly between the P treatments (Fig. 3B). The internal P utilization efficiency (PUE) decreased almost linearly as an increasing amount of P was added, from 0.29 (6 and 12 mg L^{-1}) to 0.14 (48 mg L^{-1}) g DM per mg of shoot P (Fig. 3C). PUE was closely related to PE ($r = 0.97$, $p < 0.001$).

3.2.2. *Chrysanthemum*

For chrysanthemum also, the P treatment markedly affected both total shoot uptake (Fig. 2E) and concentration of P (Fig. 2F) as well as PE (Fig. 3D) and PUE (Fig. 3F) ($p < 0.001$). The total shoot P uptake increased linearly within the P range tested ($R^2 = 0.995$, $p < 0.001$) and both the intercept with the Y-axis and the slope were similar to the values observed for poinsettia. The shoot P concentration increased

linearly from 18 to 48 mg P L^{-1}. When the 18 mg of total P estimated as necessary for optimal shoot dry matter (see 3.1) was used as a fixed breakpoint in segmented regression, the corresponding P concentration was estimated to 0.20 %. The intercept for the first segment with the Y-axis was 0.18 %. Shoot P uptake was positively related to shoot DM ($r = 0.71$, $p < 0.001$), while shoot P concentration was not ($r = 0.51$, ns). The intercept with the Y-axis for shoot P uptake indicated that 1.97 mg P was already present in the plantlets at the start of the experiment. This was subtracted from the total P uptake when PE and PAE were calculated.

Shoot PE ranged from 0.31 to 0.10 g DM mg^{-1} of P added at 6 and 48 mg P L^{-1}, respectively (Fig. 3D). While PE was similar at 6 and 12 mg P L^{-1}, it was significantly reduced by each further increase in the amount of P applied. PAE ranged from 0.54 (at 6 mg P L^{-1}) to 0.62 (at 24 mg P L^{-1}) mg shoot P per mg of P fertilizer added, but did not differ significantly between the P treatments (Fig. 3E). Shoot PUE was similar for 6 and 12 mg P L^{-1}, but decreased thereafter with an increasing level of P from 0.58 (6 mg P L^{-1}) to 0.16 (48 P mg L^{-1}) mg DM per mg P taken up in the shoot (Fig. 3F). PUE was closely related to PE ($r = 0.98$, $p < 0.001$) even for chrysanthemum.

4. Discussion

4.1. Plant ornamental quality and growth

4.1.1. Poinsettia

A significant reduction of stem and internode lengths of poinsettia 'Mira Red' was obtained only with 6 mg P L^{-1} as the concentration in the initial substrate + in the weekly fertigation solution (Fig. 1AB). Khandan-Mirkohi et al. (2015) reported that stem length of poinsettia' Premium Red' was reduced at an initial peat:mineral substrate P concentration of 10 mg P L^{-1} in comparison with 35 mg P L^{-1}. As the latter substrate treatments were combined with 20 − 30 mg P applied by fertigation during the experimental period, the 10 mg P L^{-1} treatment of Khandan-Mirkohi et al. (2015) should be comparable with our 24 mg P L^{-1} treatment (Table 1). Baas et al. (1995) observed reduced plant height at 2.8 compared with 7.4 mg P L^{-1} in the ebb-and-flow fertigation solution for poinsettia cv. 'Alstar' and 'Regina'. For zinnia (*Zinnia elegans*) and vinca (*Catharanthus roseus*) cultivated in peat:perlite 70:30 with daily fertigation containing 3.1, 6.2, 15.5, 31, 62 or 124 mg L^{-1}, maximum shoot length was obtained at 6.2 and 15.5 mg L^{-1} P in the fertigation solution (Frantz, 2013).

Reduced stem length of poinsettia has been reported also at very high P levels (Kiplinger et al., 1975; Whipker and Hammer, 1994). Testing eight poinsettia cultivars in soil:peat:perlite (1:2:2, v:v) with different initial amounts of superphosphate, Whipker and Hammer (1994) found no effect on stem length with an initial substrate P concentration in the range of 10 to 70 mg L^{-1} combined with 46 mg L^{-1} at each watering occasion. However, a small stem length decrease was observed with initial substrate concentrations higher than ca. 100 mg P L^{-1}. Similarly, plant height tended to decrease when pre-plant fertilizer P was increased from 1 to 4 times the recommended rate, increasing leaf P concentrations from 0.39 to 0.87 % (Kiplinger et al., 1975).

Not only plant height but also other factors related to the ornamental value of poinsettia, such as branching and bract diameter, were negatively affected at 6 mg P L^{-1} (Fig. 1DE). The maximum number of nodes was obtained at 12 mg L^{-1} in our experiment (data not shown), comparable with the optimal node number of *Scaevola aemula* observed at 14.5 mg L^{-1} by Zhang et al. (2004). For maximum number of lateral shoots and plant diameter, 24 mg P L^{-1} was needed in the substrate and fertigation solution (Fig. 1CD). Similarly, Khandan-Mirkohi et al. (2015) reported that both plant diameter and the number of branches of poinsettia decreased when the initial substrate P concentration was reduced from 35 to 10 mg L^{-1}. For vinca and zinnia, lateral shoot formation was optimal at 6.2 and 15.5 mg L^{-1} P, respectively, in the constant fertigation solution (Frantz, 2013).

While 12 and 18 mg P L^{-1} was sufficient for optimal bract number (data not shown) and bract diameter (Fig. 1E), respectively, both bract number and diameter tended to decrease at 48 mg L^{-1}. Reduced bract diameter at high P was reported by Kiplinger et al. (1975) for poinsettia' Annette Hegg' when the initial substrate P content was raised from 0.5 to four times the recommended rate. Whipker and Hammer (1994) also reported reduced bract diameter for some poinsettia varieties at initial substrate P concentrations from 70 mg L^{-1} + weekly addition of 46 mg P L^{-1}.

Following the increased number of lateral shoots and plant diameter, poinsettia biomass also increased with P up to 24 mg L^{-1} (Fig. 2A). Khandan-Mirkohi et al. (2015) found optimal biomass yield of poinsettia at an initial peat:mineral substrate P concentration of 35 mg L^{-1}, increasing the total amount of P applied to 55 − 65 mg which was somewhat lower than our 48 mg P L^{-1} treatment (Table 1). One factor contributing to the different results observed for poinsettia by Khandan-Mirkohi et al. (2015) and in our study could be the distribution of the P fertilizer during the cultivation period. While the total amount of P added in the suboptimal 10 mg P L^{-1} treatment of Khandan-Mirkohi et al. (2015) corresponded approximately to our optimal 24 mg P L^{-1} treatment, a larger share of the total P was given earlier in the cultivation period in our study. This may have contributed to the lower optimal P concentration found by us as a higher poinsettia P requirement has been observed at an early plant age (Khandan-Mirkohi and Schenk, 2009b). Also, comparing 1, 3, 5, 10, 20 and 30 mg P L^{-1} in the fertigation solution applied every 1–2 days to lantana grown in perlite:vermiculite 1:1, Kim and Li (2016) concluded that 20 mg L^{-1} was needed for optimal vegetative growth, while 10 mg L^{-1} was sufficient for reproductive growth. Combining 7.8 mg P L^{-1} via constant fertigation with 57 mg P L^{-1} added initially as starter P to the peat-perlite medium of poinsettia cv.' V-14 Glory', Ku and Hershey (1997) found that plants of good to premium marketable quality could be produced. For *Scaevola aemula* grown in a peat-based substrate and receiving P by fertigation two-three times per week, optimal P concentration tested for shoot number, dry matter and leaf size was 14.5 mg L^{-1} (Zhang et al., 2004). Similarly, Zinnia and vinca obtained maximum shoot biomass with 15.5 mg P L^{-1} as constant fertigation (Frantz, 2013). For New Guinea impatiens (*Impatiens hawkeri*) and vinca (*Catharanthus roseus*) grown in soilless media with recirculating subirrigation, optimal P for shoot DM was 23 and 21 mg L^{-1}, respectively (Whitcher et al., 2005).

In summary, under our fertilization scheme, 18 mg L^{-1} of P was sufficient to obtain optimal bract number and diameter and saleable poinsettia plants of acceptable quality. For maximal branching and biomass, however, 24 mg L^{-1} would be required. This corresponds to a total amount of 35 mg P, which is close to the 37 mg P that was estimated by sequential regression to be the amount of P fertilizer needed for maximal shoot biomass

4.1.2. Chrysanthemum

Similar to poinsettia, significant reduction in chrysanthemum stem length was obtained only at the lowest P level (6 mg P L^{-1}), where the other plant quality parameters measured were also negatively affected (Fig. 1F–J). In our experiment, optimal shoot number was reached already at 12 mg P L^{-1}, while 18 mg L^{-1} was necessary for optimal plant diameter. Reduced plant height, plant diameter and shoot branching at low levels of P fertilization were also observed in a chrysanthemum field experiment by Satar et al. (2016). Reduced axillary bud outgrowth and shoot branching induced by P starvation in chrysanthemum has been associated with relocation of auxin and increased contents of strigolactones (Xi et al., 2015).

The longer period before anthesis at 6 mg L^{-1} P in comparison with the other P treatments in our study confirms the results of Kageyama and Konishi (1992) of delayed flowering in P-deficient chrysanthemum plants. Also, a reduced flower number has been reported to be induced by a low availability of P for chrysanthemum (Hansen and Lynch, 1998;

Satar et al., 2016) and for a range of other ornamental plants such as petunia, pelargonium and salvia (Baas et al., 1995), vinca and zinnia (Frantz, 2013), New Guinea impatiens (Whitcher et al., 2005), *Impatiens* × *hybrida* (Justice and Faust, 2015) and *Lantana camara* (Kim and Li, 2016). In contrast, the number of flowers was not affected by low P for *Impatiens walleriana* (Baas et al., 1995). In our experiment, 24 mg L^{-1} of P in substrate and nutrient solution was necessary for optimal flower + bud production of chrysanthemum (Fig. 1J). This is lower compared with the observation of Wolz (1956) that the number of flowering buds of sand-grown chrysanthemum increased with an increasing nutrient solution P content up to 80 mg P L^{-1}. For New Guinea impatiens and vinca, optimal P for flower number was 30 mg L^{-1} and 39 mg L^{-1}, respectively (Whitcher et al., 2005). Frantz (2013) reported a lower constant rate of 15.5 mg L^{-1} P in the daily fertigation solution as optimal for flowering of both zinnia and vinca (Frantz, 2013). For *Scaevola aemula*, the number of flowers decreased only at P levels above 43.5 mg L^{-1} (Zhang et al., 2004).

Chrysanthemum DM was strongly affected by increased P fertilization from 6 to 12 mg L^{-1} but was not significantly affected by higher P concentrations (Fig. 2D). The 12 mg P L^{-1} treatment corresponded to a total amount of 15 mg P (Table 1), which is a slightly lower than the 18 mg P that was estimated by sequential regression to be the necessary amount of P fertilizer for maximal shoot biomass. Testing 0, 1.25, 2.5, 5, 10, 20, 40 and 80 mg P L^{-1} in the nutrient solution for chrysanthemum grown in sand, Wolz (1956) concluded that maximum shoot fresh weight was attained at 40 mg P L^{-1}. For chrysanthemum 'Coral Charm' grown in nutrient solution containing 0.031, 3.1 or 155 mg P L^{-1}, photosynthesis and shoot biomass decreased at 0.031 but not at 3.1, in comparison with 155 mg P (Hansen et al., 1998). The difference in P deficiency threshold levels between our experiment and the cited chrysanthemum studies is probably partly related to the difference between the cultivation systems used. In the hydroponic system of Hansen et al. (1998), the P concentration was kept low and stabilized by a solid-phase alumina-P buffer, while the substrate P concentrations in our pot experiments could be expected to decrease from the start of the trials and then fluctuate between the weekly fertilization occasions.

4.2. Shoot P concentration

4.2.1. Poinsettia

The lowest shoot P concentration (Fig. 2C) observed for poinsettia in the present study, 0.24 % of shoot DM, was close to the minimum critical foliar P level of 0.2 % reported for adequate plant growth of poinsettia (Kiplinger et al., 1975; Winsor and och Adams, 1987). The intercept with the Y-axis at 0.21 % in our study (Fig. 2C), interpreted as the minimum critical P concentration for growth of poinsettia, is also in accordance with the critical value reported above. A normal leaf P concentration range for poinsettia of 0.35-0.75 % has been reported (Winsor and och Adams, 1987). Mills and Benton Jones (1996) presented 0.20–1.00 % as the sufficiency range for poinsettia in the period from bract coloration to flowering. The estimated optimal shoot concentration of 0.35 % for shoot DM in the present study is in accordance with the normal ranges reported above, but lower compared with the optimal concentration of 0.5-0.6 % for shoot DM of poinsettia cv.' Premium Red' reported by Khandan-Mirkohi & Schenk (2009a). Differences between genotypes and sampling times may affect poinsettia foliar P concentrations (Whipker and Hammer, 1994) and may have contributed to the differences in the suggested optimal P ranges for growth of poinsettia.

Optimal bract diameter (Fig. 1E) was obtained at 0.32-0.34 % shoot P (Fig. 2C) which is within the leaf P range of 0.3-0.5 % suggested as desirable for optimal bract diameter by Kiplinger et al. (1975). This is also in accordance with Ku and Hershey (1997) who observed premium quality at 0.31-0.38 % foliar P for poinsettia 'V-14 Glory', while luxury P consumption in the 0.53-0.72 % range increased neither shoot dry mass nor leaf or bract area. In our study, bract diameter even tended to decrease at 0.58 % shoot P (48 mg P L^{-1}).

4.2.2. Chrysanthemum

The lowest P shoot concentration (Fig. 2F) sustaining chrysanthemum 'Breeze cassis' growth in our experiment was 0.19 %, which is similar to the critical leaf concentration for P deficiency of 0.20 % reported by Winsor and och Adams (1987). The observed intercept with the Y-axis in our study suggests a minimum critical P concentration of 0.18 % for growth of chrysanthemum. At 12 mg P L^{-1}, the increased P supply compared with 6 mg P L^{-1} supported both a markedly greater biomass and a maximum plant length at 0.20 % shoot P. Winsor and och Adams (1987) suggested 0.30-0.80 % leaf P as the normal range for chrysanthemum, while Mills and Benton Jones (1996) presented 0.20–1.20 % as the sufficiency range from bud set to harvest. For the cultivars 'Delaware' and 'Oregon', optimum biomass of mature chrysanthemum plants was reported at 0.18 and 0.24 % foliar P, respectively (Waters, 1964). In our study, increasing the P treatment from 18 (0.25 % P) to 24 or 48 mg L^{-1} did not affect plant biomass but increased total uptake of P, resulting in shoot P concentrations of 0.30-0.35 % and 0.57-0.58 %, respectively. As higher leaf than stem concentrations have been reported for chrysanthemum in both the vegetative and the generative stage (Hansen and Lynch, 1998), our whole-shoot concentrations may correspond to somewhat higher leaf concentrations. Furthermore, genotypes may respond differently to P. While the foliar P concentration increased linearly for 'Oregon', 'Delaware' showed a quadratic response (Waters, 1964).

4.3. Shoot P accumulation and P efficiency

The decreasing shoot growth response as the amount of P fertilizer increased (Fig. 2A, D) was also reflected in a lower shoot phosphorus efficiency (PE) (Fig. 3A, D). Decreasing PE with increasing P fertilization is commonly observed for agricultural crops (Syers et al., 2008). In our study, the decrease was most evident for chrysanthemum, starting at a markedly higher PE than poinsettia at the lower P treatments. Our PE of 0.16 (poinsettia) and 0.31 (chrysanthemum) g DM mg^{-1} P at 6 mg P L^{-1} were in similar ranges as the PE values of 0.23 and 0.37 g DM mg^{-1} P reported by Frantz (2013) for vinca and zinnia, respectively, at 3 mg P L^{-1} in the fertigation solution. Also, our PE values at 48 mg P L^{-1} (0.08-0.10 g DM mg^{-1} P) agreed with the PE observed for vinca and zinnia when the fertigation solution P was increased from 3 to 15.5 (vinca) and 31 (zinnia) mg L^{-1} (Franz 2013). The optimal PE for zinnia of just below 0.2 g biomass mg^{-1} P suggested by Frantz (2013) corresponds well with the PE values observed at the optimal P levels of 0.2-0.3 g biomass mg^{-1} P for chrysanthemum (at 12 − 18 mg P L^{-1}) and 0.15 g for poinsettia (at 18 − 24 mg P L^{-1}) in the present study.

The total shoot P uptake increased linearly with an increasing amount of P applied, with similar slopes for both species (Fig. 2B, E). The concomitant slow increase in shoot P concentration up to 12 mg L^{-1} (chrysanthemum) and 24 mg L^{-1} (poinsettia) suggests that most of the P taken up was used to sustain the linear increase in shoot growth (Fig. 2C, F). At 48 mg P L^{-1}, however, the strong increase in shoot P concentration combined with the absence of shoot biomass response indicated luxury consumption of P. Luxury P consumption was also observed for poinsettia when the P concentration in the fertigation solution was increased from 7.8 to 11 to 22 − 23 mg L^{-1} (Ku and Hershey, 1996; 1997). Similarly, while lantana whole-plant and shoot P content and concentration increased strongly when the nutrient solution P was increased from 10 to 20 mg L^{-1}, the higher P accumulation in plant tissues at 30 mg L^{-1} did not contribute significantly to biomass production (Kim and Li, 2016). Frantz (2013) reported luxury consumption by zinnia when the P supply in the daily fertigation solution was increased from 15.5–31 mg L^{-1}. For vinca, however, the uptake of P closely followed shoot growth and no luxury uptake was observed (Frantz, 2013).

The mean shoot phosphorus acquisition efficiency (PAE, Fig. 3B, E), corresponding to 55 and 58 % recovery of the total amount of P applied during the poinsettia and chrysanthemum experiment respectively, was higher than the 35–40 % shoot PAE reported at low P levels by Frantz (2013) for vinca and zinnia. For container-grown azalea, total plant PAE was in the range of 41–49 % at low P (5 mg week^{-1}) and 11–15 % at high P (25 mg week^{-1}) (Ristvey et al., 2007). As leakage from the pots was restricted in all studies mentioned above, the higher PAE in our study was probably related to a more limited supply of P in relation to the requirement of the plants.

The general decrease in shoot internal phosphorus utilization efficiency (PUE) with an increasing amount of P in the nutrient solution for chrysanthemum, and at 48 mg P L^{-1} for poinsettia (Fig. 3C, F), also demonstrated that as more P was taken up in the shoot, a smaller proportion was utilized for growth (Fig. 2A, D). As P becomes less limiting, a larger fraction will be stored as inorganic P in the vacuoles to maintain cytosol P homeostasis (Yang et al., 2017).

PUE in the optimal P fertilization range was about 0.4-0.5 g DM mg^{-1} P (12 – 18 mg P L^{-1}) for chrysanthemum, which was markedly higher compared with the 0.26 g mg^{-1} (18 – 24 mg P L^{-1}) for poinsettia. For poinsettia, this was similar to the PUE recalculated from Ku and Hershey (1997) of about 0.3 g DM mg^{-1} P for mature 'V-14 Glory' poinsettia leaves at optimal plant quality. In contrast, for the optimal shoot P concentration range of 0.5-0.6 % for poinsettia 'Premium Red' reported by Khandan-Mirkohi and Schenk (2009a), PUE could be estimated to 0.17-0.20 g DM mg^{-1} P. This is close to the PUE observed at luxury P levels of 0.14-0.16 and 0.14-0.19 g DM mg^{-1} P observed by us and recalculated from Ku and Hershey (1997), respectively.

The markedly higher PUE observed for chrysanthemum (0.52-0.58 g DM mg^{-1} P) than for poinsettia (0.29 g DM mg^{-1} P) at the two lower P levels suggests a lower tissue P requirement for chrysanthemum growth. This was confirmed by the almost double slope for shoot dry matter against the total amount of P applied (0.31 g DM mg P^{-1}, Fig. 2D) of chrysanthemum in comparison with poinsettia (0.14 g DM mg P^{-1}, Fig. 2A) for the first linear part of the curve. As P was included in the fertigation solution from DAP 28 for chrysanthemum and from DAP 36 for poinsettia, the chrysanthemum plants grown at low P might have experienced a less intensive early P limitation compared with poinsettia low-P plants. Hence, it cannot be excluded that a better early P status might have contributed to the lower total P requirement observed for chrysanthemum than for poinsettia growth.

Even if less than 60 % of the P applied was consumed by the shoots, periods of P depletion in the root zone during early plant growth cannot be excluded. Khandan-Mirkohi and Schenck (2009a) calculated P depletion profiles for poinsettia roots from 10 DAP and showed that after two days of depletion, the concentration at the root surface was below the estimated K*m* value when 0 or 10 mg P L^{-1} was the initial substrate P concentration. They concluded that for these two P treatments, the P concentration gradients were insufficient to fill the demand. Hence, at least for our poinsettia plants, where fertigation also started later than for chrysanthemum, the P limitation experienced at the lower P levels may have been accentuated during the early cultivation period by a low root density and thus by a limited ability of the roots to fully exploit substrate P.

Morphological plant root adaptions to low P conditions have been observed for both chrysanthemum (Hansen and Lynch, 1998) and poinsettia (Khandan-Mirkohi and Schenk 2009a). Also, a low-affinity P transporter affecting both P uptake and root biomass has been shown to be induced in chrysanthemum roots under low P conditions (Liu et al., 2014, 2018). Physiological root P uptake characteristics have been suggested to be more important for P acquisition than root morphological attributes in peat substrates where the mobility of P is high (Khandan-Mirkohi and Schenck, 2009a). However, the lack of significant correlation between PE and PAE suggests that neither root morphological nor physiological uptake characteristics were decisive for plant response to P limitation in the present study. This is supported by the close correlation between PE and PUE, suggesting that internal plant utilization was more important than root uptake characteristics in plant adaption to the P limitation imposed in our study.

From the discussion above, it follows that a low P concentration in the soil solution could sustain plant growth as long as it is kept constant (Hansen and Nielsen, 2001), maintaining the P concentration gradient in the root zone. For chrysanthemum, a constant concentration of 3.1 mg L^{-1} in the hydroponic nutrient solution was regarded as sufficient (Hansen and Lynch, 1998). For poinsettia and marigold grown in a peat-based substrate, the optimal concentration of P in the substrate solution was as low as 1.5 mg L^{-1} (Khandan-Mirkohi & Schenk 2009a). Hence, for production of ornamental plants at a reduced P supply, maintaining a constant soil solution P concentration is important.

4.4. Conclusion

Even if a more gradual increase in shoot biomass with increasing P supply was evident for poinsettia (Fig. 2A), a significant plant height reduction was observed at 6 mg P L^{-1} only for both species (Fig. 1A, F). Due to the concomitant strong reduction of flower bud or bract number and diameter and lateral shoot formation at this P level, however, restriction of P supply did not seem to be a feasible method for plant height control neither for chrysanthemum nor for poinsettia.

For both plant species, it was clear that when using a combination of fertilized substrate and supplemental fertilization during the cultivation period, a P concentration of 18 – 24 mg P L^{-1} would be enough for the production of good to high quality plants. Hence, for optimizing both shoot DM and ornamental quality, the shoot P concentration at 90 DAP should be in the range of 0.30-0.35 % (poinsettia) and 0.25-0.30 % (chrysanthemum). However, saleable plants of acceptable quality, but with fewer branches (both species) and flowers (chrysanthemum), were produced at 12 mg P L^{-1} for chrysanthemum and at 18 mg L^{-1} P for poinsettia. While the *optimal* shoot P concentrations for shoot DM production were estimated by segmented regression to 0.35 % (poinsettia) and 0.20 % (chrysanthemum), the *critical* P concentrations for shoot biomass were estimated to 0.21 % for poinsettia and 0.18 % for chrysanthemum in our study.

Chrysanthemum showed a higher PE than poinsettia at low P levels. This was due to a higher PUE, indicating a better ability of chrysanthemum to adapt the internal P utilization to a limited availability of P. Generally, more information is needed on the response to restricted P supply, PAE and PUE of ornamental plants. The influence of different P fertilization strategies on plant quality and P recovery should also be studied to increase the P efficiency of ornamental plant production. Limiting excessive P supply in horticultural substrates and nutrient solutions is important for using phosphorus fertilizer more efficiently. This would lead to reduced risks of leakage and an increased quality/cost ratio; improving both environmental and economical sustainability of the ornamental plant industry.

CRediT authorship contribution statement

Siri Caspersen: Conceptualization, Methodology, Investigation, Writing - original draft, Formal analysis, Visualization, Funding acquisition. **Karl-Johan Bergstrand:** Conceptualization, Methodology, Investigation, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

No interests to declare.

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